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Department of Microbiology, Molecular Biology and Biochemistry, University of Idaho, MMBB LSS142, Moscow, Idaho 83844-3052, USA.
E-mail: dcole@uidaho.edu

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Evolutionary Conflict: Sperm Wars, Phantom Inseminations

A new experimental study has provided the first definitive evidence for conditional punishment of 'cheats' in a sperm-trading simultaneous hermaphrodite: the sea slug *Chelidonura hirundinina*. This also provides a rare unequivocal example of conditional reciprocity averting a 'tragedy of the commons' in biology.

Sasha R.X. Dall and Nina Wedell

Conflicts of interest abound in biology. Indeed, from a neo-Darwinian, gene selectionist perspective many biological phenomena owe their existence to the evolutionary outcome of conflicts of interest between entities with independent reproductive lineages. Consider genomic imprinting, for instance, whereby genes inherited from fathers show different patterns of expression to those inherited from mothers [1]. In taxa with substantial maternal investment in offspring and multiple paternity, paternally inherited genes will be selected to cause young to solicit more than their fair share of the maternal investment. This is because such selfishness is unlikely to impact negatively on the success of other copies of the genes, as the mother of a current offspring is also likely to invest in offspring sired by other males. This will not be the case for genes inherited maternally. There is therefore potential conflict between the paternally and maternally inherited genes, which is consistent with the available data on patterns of expression of imprinted genes in mammals and plants [2,3].

From a broader perspective, despite there often being substantial benefits to coordinated action — from genes coordinating with each other to develop bodies to lionesses synchronizing their hunts to take large savannah ungulates — achieving such cooperation presents problems. To enjoy a common good, individuals must often take on the risk of investing resources in a communal pool without guaranteed returns. This sets up the potential to free-ride — accept resources from the pool without investing anything in return. It is the risk of being 'suckered' by free-riders that can so easily bind organisms to the 'tragedy of the commons', whereby the common good is sacrificed because of the potential for individuals to cheat. In fact, the burden of explanation often falls on those instances where the tragedy of the commons seems to have been averted in biology. One example of this is the case of achieving the benefits of sexual reproduction [4] when there are conflicts over gender roles in simultaneous hermaphrodites such as the sea slug, *Chelidonura hirundinina,* the subject of a new study by Anthes and co-workers reported in this issue of *Current Biology* [5].

With the evolution of distinct male and female roles in sexual reproduction — anisogamy — an important source of evolutionary conflict of interest was born [6]. For a fixed level of investment in reproduction, mating partners that consistently invest more in providing young with start-up resources will turn out fewer reproductive attempts in their lives with a greater interest in the fate of each. This means that such mating partners — females — should be relatively choosy about the circumstances surrounding each such event. On the other hand, with less investment in each potential reproductive event, males can attempt many more matings, but they face the problem of winning rights to the limited opportunities to access the choosy females and their rare eggs.

This difference creates divergent interests in the mating game, with males being selected to coerce their partners into reproducing and females to resist such overtures [6]. It also means that females can virtually guarantee that their eggs will be fertilized at some point in their lives, while males face no such surety for any of the sperm they produce. Nevertheless, despite such divergence in interests and mating tactics, at least some degree of coordination between the sexes is required to achieve the common good of successful sexual reproduction. For the vast majority of sexual taxa with distinct genders, the most basic level of coordination — who plays 'female' and who plays 'male' — is fixed at any given mating opportunity and beyond the potential for conflict. But this is not necessarily the case in simultaneous hermaphrodites [7], those taxa, including many species of molluscs, in which individuals can either mate as a male (by donating sperm) or a female (by receiving sperm) in any particular copulation.

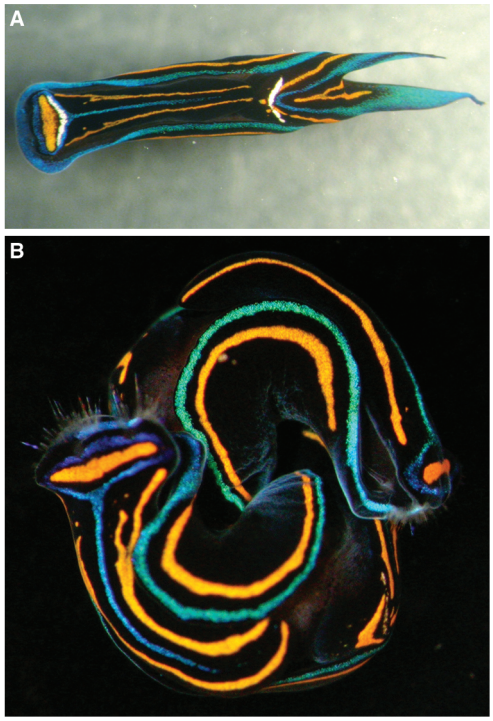

Figure 1. *Chelidonura hirundinina.*
(A) A single individual; and (B) a copulating pair.

For simultaneous hermaphrodites, a conflict of interest between mating partners emerges if there is a clear, mutual preference to adopt a particular gender role at any given copulation [7]. In internal fertilizers with limited control over the fate of their sperm, most ejaculates received will be surplus to the fertilisation requirements of an individual's eggs, so donating sperm (playing male) will only rarely confer any reproductive benefit. Instead, by playing female, individuals can get their eggs fertilised *and* potentially obtain nutrients by digesting surplus ejaculates. This can set up a universal preference to receive sperm in any given copulation.

But mutual adoption of this preferred female role during mating interactions would lead to the break down of hermaphrodite sex, as no sperm would ever be exchanged! Instead, researchers have postulated that, in order to evolve and persist, sex between simultaneous hermaphrodites must involve tactics to ensure such a 'tragedy of the commons' is averted. A simple tactic that can lead to the evolution of cooperative outcomes in a wide range of circumstances involves so-called *conditional reciprocity* [8]. In the current context, this would involve hermaphrodites trading sperm reciprocally and punishing cheaters who refuse to play the less rewarded role by desertion. Indeed, formal theoretical treatments predict that extended mating interactions with multiple inseminations and individuals trading roles (sperm) reciprocally should be observed where hermaphrodite sex persists [9].

Until now, evidence in favour of such a theory has been limited to observations of apparent alternation in sex roles during extended matings between pairs of hermaphroditic molluscs [10–14]. There is also some evidence of reciprocal sperm exchange. For example, in the sea slug *Navanax intermis*, mating partners repeatedly alternate sperm donation [7,15], and in planarian flatworms, individuals match the volume of sperm they transfer to each other reciprocally [16,17]. Although suggestive, such evidence is far from definitive in favour of conditional reciprocity as underpinning the evolution and maintenance of hermaphroditic sex — the crucial prediction of conditional punishment of cheats via desertion had not been demonstrated. The new study by Anthes *et al.* [5] provides such definitive evidence for the first time.

One of the major stumbling blocks to providing unequivocal evidence of conditional reciprocity in sperm trading by simultaneous hermaphrodites has been the ability to distinguish punishment by desertion from the termination of mating interactions for other reasons. This is where cephalaspid sea slugs such as *C. hirundinina* offer a unique opportunity: these hermaphroditic molluscs possess an external skin fold (sperm groove), along which semen flows from the genital aperture (gonopore) to the penis for insemination via intromission into a mating partner's gonopore (Figure 1). By cauterising this sperm groove, Anthes *et al.* [5] were able to block sperm donation in experimentally determined 'cheaters', whose overall penis intromission behaviour was unaffected compared to controls with skin cauterised near their grooves. So by measuring the difference in mating behaviour of experimentally imposed partners of cheaters and comparing them to the partners of controls, this study was able to establish unequivocally the consequences of withholding sperm per se during mating interactions. Indeed, Anthes *et al.* [5] provide clear evidence that these sea slugs punish conditionally by showing that partners of the experimentally determined 'cheats' are relatively reluctant to 'play male' and tend to terminate mating sequences early.

But not all simultaneous hermaphrodites employ the conditional punishment of cheats to manage sexual interactions. In some cases there appears to be no conflict over gender roles at all. For example, in the closely related *C. sandra*, mating partners show mutual willingness to donate sperm reciprocally and experimental cheats to do not incur any penalty [18]. Moreover, when there are significant costs associated with sperm receipt, as with hypodermic insemination and the associated costs of wound healing in the flatworm

Pseudocerus bifurcus, behaviours such as penis-fencing are favoured to avoid receiving sperm [19]. Thus, the opposite pattern of a universal preference for playing the male role can also emerge.

Nevertheless, the work of Anthes *et al.* [5] is exceptional in providing definitive evidence for sperm trading in hermaphroditic sexual reproduction. Moreover, this work provides clear evidence of male 'mate choice' in the form of selective sperm donation to 'honest' partners. Alone, such features should earn this study a place in the text books; more so since it also provides a rare unequivocal example of conditional reciprocity being employed to escape the tragedy of the commons in biology.

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Centre for Ecology & Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn TR10 9EZ, UK. E-mail: sashadall@iname.com

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Plant Meristems: Mobile Mediators of Cell Fate

How do transcription factors control the fates of cells that express them? One class of plant transcription factors has recently been shown to function by regulating the synthesis of cytokinin and gibberellin hormones — mobile molecules more usually associated with long-distance signalling.

Andrew Hudson

Cell fates at the apex of plant shoots are controlled by homeobox transcription factors of the KNOX-I family. *KNOX-I* genes act as selectors of meristem cell identity; their activity is needed to distinguish cells of the shoot apical meristem (SAM) from those of leaves (Figure 1A), and ectopic *KNOX-I* expression can confer SAM-like identity on leaves. For any transcription factor that controls cell identity, one major question is how that identity is realised through regulation of target genes. Two papers [1,2] published recently in *Current Biology* report evidence that two plant hormones, gibberellin and cytokinin, together mediate the KNOX-I control of SAM cell identity.

Control of cell fate in the SAM has long been known to involve *KNOX-I* genes. *KNOX-I* expression is characteristic of the SAMs of diverse land plants [3] and is lost from peripheral cells as they are specified as leaf initials (Figure 1B). For example, activity of the *KNOX-I* gene *SHOOT MERISTEMLESS* (*STM*) is needed to prevent cells of the *Arabidopsis* apex expressing leaf genes and differentiating, giving rise to embryos without SAMs [4]. Conversely, ectopic *STM* expression in developing leaves confers characteristics of the peripheral SAM and is sufficient to specify complete SAMs when expressed ectopically with the distantly related transcription factor WUSCHEL, which promotes central cell identity [5].

Earlier work [6] had shown that STM is needed in the SAM to maintain low gibberellin levels and inhibit expression of the *GA20-ox1* gene, which encodes a rate-limiting enzyme of gibberellin biosynthesis. *GA20-ox1* expression is normally confined to leaves, where gibberellin levels are high, but exluded from the apex by STM activity. Two lines of evidence suggested that repression of *GA20-ox1* by STM is functionally relevant. Firstly, the interaction is likely to be direct — KNOX-I protein can bind a regulatory sequence in the GA-20 oxidase gene of tobacco [7]. Secondly, the effects of KNOX-I activity are partly dependent on an ability to respond to gibberellin. For instance the *spindly* (*spy*) mutation, which mimics high gibberellin levels by allowing a constitutive gibberellin response [8], enhances the effects of weak *stm* mutations and